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Holocene environmental change in the eastern Snake River Plain of Idaho, USA, as inferred from stable isotope analyses of small mammals

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ABSTRACT

Previous research on the small mammal population recovered from archeological excavations at the Wasden Site in southeastern Idaho suggests that changing frequency distributions through time represent a shift in climate during the early Holocene from a cooler, wetter regime to a warmer, drier one. This conclusion was re-evaluated using stable carbon and nitrogen isotope analyses of bone collagen from the three species of small mammals examined in the earlier studies: pocket gophers (*Thomomys talpoides*), pygmy rabbits (*Brachylagus idahoensis*), and ground squirrels (*Spermophilus townsendii*). Resulting carbon and nitrogen isotopic values are consistent with known differences in feeding ecology, suggesting high fidelity as proxies for past vegetation (and thus climate) regimes. Patterns of ^{15}N enrichment and increased representation of C_4-CAM vegetation observed in the pocket gophers, and to a lesser extent ground squirrels, suggests increasing warmth and/or aridity from the early Holocene until ~7000 cal yr BP, thus supporting previous hypotheses of climate change on the eastern Snake River Plain. The results highlight the potential contribution of such studies for archeological research by providing additional proxies for environmental conditions that bear on paleoecological adaptations to climatic change, including past human use and occupation of the region.

Introduction

The stable isotopes of carbon and nitrogen in terrestrial animal bone collagen provide valuable information about past environments, including changes in variables such as temperature, moisture, salinity, and vegetation. While most previous studies focus on larger bodied mammals (e.g., Ambrose and DeNiro, 1989; Iacumin et al., 2000; Richards and Hedges, 2003; Drucker et al., 2003a, 2003b), fewer studies explore the potential of carbon and nitrogen isotopic compositions of small mammals, e.g., rodents and lagomorphs, for understanding climate and vegetation changes (though see Rogers and Wang, 2002; Ugan and Coltrain, 2011; Gasiorowski et al., 2013). Here, we examine a museum collection of small mammal material excavated from the Wasden Site, southeast Idaho, USA, in the 1960s and 1970s to determine its utility in reconstructing past environments on the eastern Snake River Plain.

Background

Small mammals as paleoenvironmental indicators

Small mammal assemblages created through natural processes such as deposits accumulated by nocturnal raptors, i.e., owls, or woodrats, are excellent proxies for local climate and vegetation change (e.g., Andrews, 1990; Grayson, 2000; Hopley et al., 2006; Reed, 2007; Terry, 2008a,b; 2010a,b). Due to their size, small mammals generally have restricted home ranges, and as such are sensitive to environmental fluctuations; if perturbations are too large, populations cannot survive and will migrate or expire. Thus, the presence/absence or changing frequencies of small mammals in the stratigraphic record reflects changing environmental conditions. In addition, avian predators such as owls have relatively narrow hunting ranges (Andrews, 1990; Terry, 2008b, 2010a, 2010b). Small mammal skeletal assemblages accumulated by such predators, therefore, should reflect the composition of the animals within the local foraging area at specific points in time.

The environmental sensitivity of small mammals and the spatial control of naturally accumulated skeletal material have allowed

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researchers to develop fine-scaled reconstructions of past environments through analyses such as species counts, distributions and morphological changes (e.g., Vigne and Valladas, 1996; Hadly, 1997; Hadly et al., 1998; Cuenca-Bescos et al., 2009; Arzu et al., 2011). Although such analyses provide valuable information, deposits with adequate abundances of well-preserved small mammal remains are the exception rather than the norm. Fortunately, methods such as stable isotope analysis, which do not require the large sample sizes of these more traditional faunal analyses, may provide additional vital data sources. Carbon and nitrogen isotopic ratios within animal tissues are determined by the composition of the food they consume. Therefore, environmental changes that affect the physical characteristics of vegetation communities, e.g., changes in key species or overall distributions, and/or their stable isotope composition should also be reflected in changes in the isotopic composition in animal tissues, especially those of herbivores.

The Wasden Site

The Wasden Site is a significant archeological and ecological site on the eastern Snake River Plain in southeastern Idaho (Fig. 1). Based on the artifact catalogs curated with the collection at the Idaho Museum of Natural History (IMNH), approximately 10,000 yr of human activity is represented within the cave deposits, with over 2000 artifacts-including lithic tools and debitage, bone tools and worked pieces, shell, pottery and textile fragments-found throughout the stratigraphic sequence (IMNH Accession File 1642.2). More than 10,000 bones of large mammals (primarily bison), and at least five times as many small mammal bones have been recovered (IMNH Accession File 1642.2).

The site is located between the Idaho National Laboratory and Idaho Falls, Idaho and lies at an elevation of about 1432 m above sea level (Fig. 1). This general area falls within the Lava Fields and Eastern Snake River Basalt Plain Level IV ecoregion identified by the United States Environmental Protection Agency for the Snake River Plain (McGrath et al., 2002). These ecoregions are characterized by a mixture of exposed basalt and shallow soils, low surface water availability, and sagebrush steppe as the dominant plant community. Currently, the site lies within fields of crested wheatgrass (*Agropyron cristatum*), though small stands of the sagebrush steppe plant community survive on a nearby butte and in small patches interspersed throughout the agricultural area. Some plants observed in more undisturbed areas around the site in June 2011 include big sagebrush (*Artemisia tridentata*), three-tip sagebrush (*Artemisia tripartita*), grey rabbitbrush (*Ericameria nauseosa*), prickly pear cactus (*Opuntia polyacantha*), orange globemallow (*Sphaeralcea munroana*), wild aster (*Aster* sp.), milkvetch (*Astragalus* sp.), desert paintbrush (*Castilleja angustifolia*) and hooker's onion (*Allium acuminatum*).

Precipitation for the Idaho Falls area varies seasonally with the highest average levels typically occurring in spring and a water deficit present throughout the summer (Fig. 2). Based on data for the period between 1948 and 2015 the average precipitation values by season are: 54.4 mm for winter (December, January, February); 75.7 mm for spring (March, April, May); 58.2 mm for summer (June, July, August); and 59.9 mm for fall (September, October, November) (Western Regional Climate Center, 2015, Station 104457). Average annual precipitation across this same time period is 248 mm, with the highest averages of 33.3 mm in May and 29.2 mm in June, and the lowest average of 11.9 mm in July. Average temperature by season are: −5.8 °C for winter; 6.5 °C for spring; 18.5 °C for summer; and 7.3 °C for fall. In all, the annual average temperature is

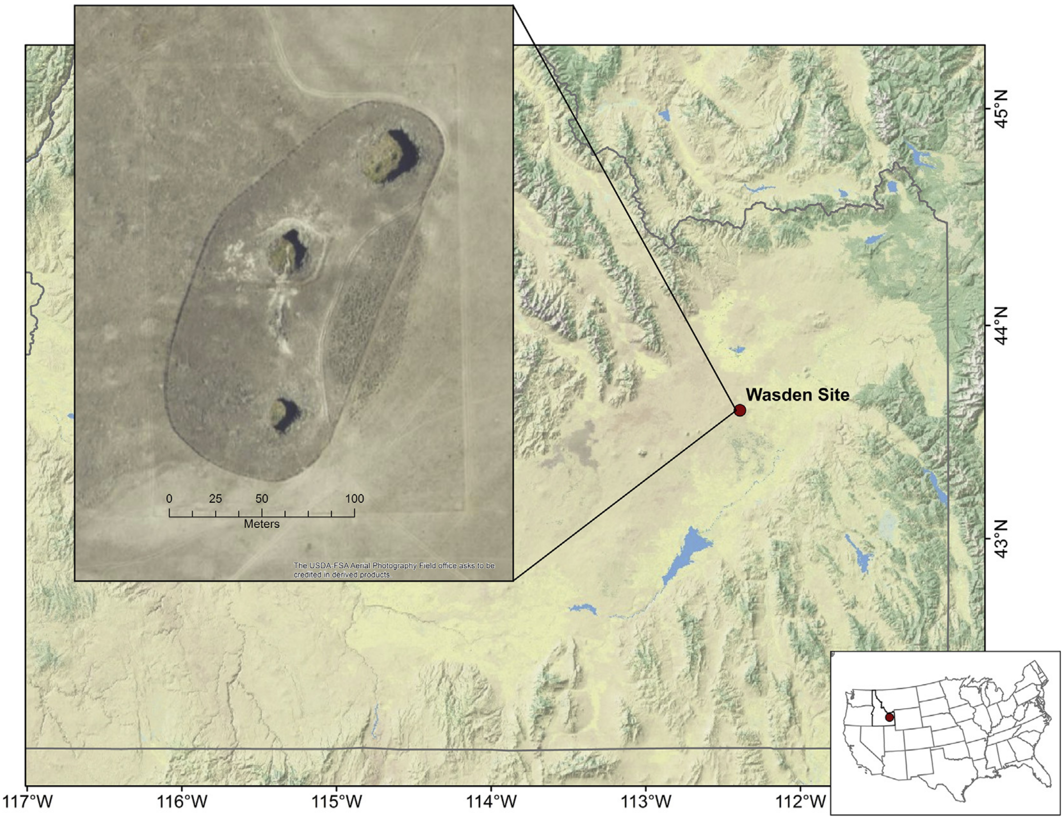

Figure 1. Location of the Wasden Site in southeastern Idaho. Inset is an aerial image of the three collapsed portions of the lava tube; Owl Cave is the central cave.

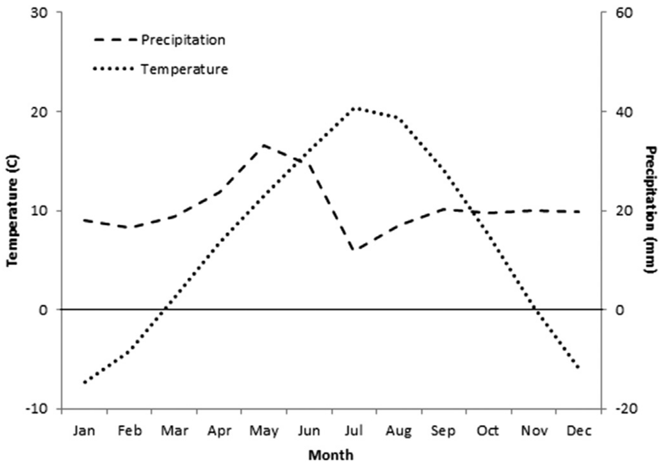

Figure 2. Average temperature and precipitation by month based on data from 1948 to 2015. Source: Western Regional Climate Center - http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?id4457: General Climate Summary Tables for Temperature and Precipitation, Station 104457 (Idaho Falls Fanning Fld [Regional Airport]), last updated March 12, 2015.

6.6 °C, with a highest monthly average of 20.3 °C in July and a lowest monthly average of −7.3 °C in January.

The Wasden site consists of three adjacent collapsed portions of what is likely a single lava tube, of which only one, Owl Cave, has been extensively excavated (Fig. 1). Field investigations were conducted between 1965 and 1977, and half of Owl Cave was excavated in 2 × 2 m blocks, using controlled, 10-cm increments within stratigraphic layers, and screened using ¼ to ⅛ inch mesh sizes. Unfortunately, there is no comprehensive report describing the excavations, so researchers must rely on the extensive field notes, maps, and correspondence, as well as numerous publications pertaining to certain aspects of the site (Butler, 1968, 1969, 1971, 1972, 1986; Guilday, 1969; Butler et al., 1971; Dort and Miller, 1977; Miller, 1982, 1983, 1989) to reconstruct the context of the recovered artifacts and faunal material.

Excavations in Owl Cave reached a depth of approximately 5 m. The lowest layer produced fragmented remains of a mammoth, camel, dire wolf, and bison along with Folsom points (Dort and Miller, 1977; Miller, 1982, 1989; Butler, 1986). At ~2 m below the surface, a bone bed dating to 8880 cal yr BP was encountered where over 7000 complete and fragmented bone elements of bison were recovered, representing over 50 individuals of both *Bison antiquus* and *B. bison* (Butler, 1968, 1971, 1972; Butler et al., 1971; Miller, 1983). Numerous artifacts above this bone bed denote human occupation during the late Holocene. The presence of fire hearths, bone tools, projectile points, stone tools, pottery, shell and bone beads, and groundstone implements suggest long-term, though sporadic use of the cave into Late Prehistoric/Protohistoric times.

In addition to the cultural components, and of specific interest to this study, is a thick deposit of small mammal material accumulated through continuous owl roosting activity over a long period of time. We chose to examine this material for several reasons: based on the field and laboratory notes excavations were conducted in 10 cm increments, implying good provenience and stratigraphic control; bone preservation is excellent, making the material suitable for a wide variety of morphological and biochemical analyses; there are more than 7000 individuals represented, providing an excellent sample size with which to examine temporal change; and, most importantly, the collection spans nearly the entire history of prehistoric use of the cave, currently thought to be at least 10,000 yr, providing a record of climate and environmental change corresponding with human occupation of the eastern Snake River Plain.

Previous research

There have been relatively few studies on this small mammal collection; in fact, only two have been published to date (Butler, 1969; Guilday, 1969). The research of Guilday (1969) consisted of identifying specimens to the species level, and examining change in species abundance through time. Based on mandible counts, Guilday (1969) estimated a minimum number of 7248 individuals, including a relatively large number of pocket gophers (*Thomomys cf. talpoides*), pygmy rabbits (*Sylvilagus[Brachylagus] idahoensis*), and ground squirrels (*Spermophilus townsendii*), and smaller numbers of cottontail rabbit (*Sylvilagus nuttallii or audubonii*), least chipmunk (*Eutamias minimus*), grasshopper mouse (*Onychomys cf. leucogaster*), weasel (*Mustela f. frenata and/or erminea*), and others. Focusing on material recovered from one portion of the site, Block E2B, he made two observations: 1) there was a marked decline in total small mammal count above a layer of Mazama Ash dating approximately 7550 cal yr BP (Hallett et al., 1997; Zdanowicz et al., 1999) relative to periods before; and 2) the most dramatic decline was in the number of pocket gophers. Guilday (1969) interpreted this as potential 'progressive desiccation' post-Mazama.

Butler (1969) used Guilday's (1969) data to evaluate the changing ratio of pocket gophers to pygmy rabbits through time. He found pocket gophers dominated the assemblage before the Mazama deposit, while pygmy rabbits were the more abundant species post-Mazama. Based on different habitats and feeding patterns reported for these animals – pocket gophers thrived in cooler, moister climates dominated by grasses, whereas pygmy rabbits flourished in sagebrush habitats indicative of warmer, more arid climates – Butler (1969) suggested a change from a cooler, wetter environment to warmer, drier one. Evidence from the sediment profile in support of this conclusion is the marked number of fossil ice wedges prior to the Mazama deposit. These were taken to indicate multiple freeze-thaw events; the profile above the Mazama deposit does not show the same phenomena, which may imply a colder climate prior to 7550 cal yr BP.

To expand on these studies, we examine the stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic composition of bone collagen from three species (Northern Pocket Gophers [*T. cf talpoides*], Pygmy Rabbits [*B. idahoensis*], and Townsend's Ground Squirrels [*S. townsendii*]) recovered from the Wasden site with the hypothesis that the climate changes proposed by Butler (1969) and Guilday (1969) would be reflected in changes in the $\delta^{13}C$ and $\delta^{15}N$ values through time.

Stable isotopes

While previous work at this site suggests environmental changes occurred during the Holocene based on observed fluctuations in specific animal populations (Butler, 1969; Guilday, 1969), stable isotope data may provide additional insight into these changes and how animal populations responded. For instance, while the previous studies inferred a shift in the proportions of grasses to sagebrush with increasing aridity, stable isotope compositions of the bones themselves may allow us to detect changing vegetation patterns, and provide information about the plants these herbivores were eating. The utility of stable nitrogen and carbon isotopes recovered from animal bone collagen in paleoenvironmental reconstructions has been presented in detail in previous and recent literature (e.g., Peterson and Fry, 1987; Ambrose, 1991; Koch, 1998; Fry, 2006; Hedges et al., 2006;

Schwarcz and Schoeninger, 2011), and relevant points are discussed briefly here.

Nitrogen

In addition to serving as trophic level indicators, increases in plant $\delta^{15}N$ values have been attributed to soil ^{15}N enrichment, increasing temperatures, decreasing rainfall abundance and/or decreasing soil moisture (DeNiro and Epstein, 1981; Ambrose, 1986, 1991; Ambrose and DeNiro, 1986; Heaton et al., 1986; Sealy et al., 1987; Evans and Ehleringer, 1994; Cormie and Schwarcz, 1996; Handley et al., 1999; Vanderklift and Ponsard, 2003). In a global review, Craine et al. (2009) found a general negative relationship between $\delta^{15}N$ values and mean annual precipitation and a positive relationship with mean annual temperature. Generally, plants in hotter, drier climates tend to have higher $\delta^{15}N$ ratios. They also noted a positive relationship between $\delta^{15}N$ values and N supply, with warm, dry sites having relatively greater N supply than cooler, wetter ones.

Previously, animal physiological processes associated with drought-adaptation were thought to contribute to increases in herbivore $\delta^{15}N$ values (e.g., Sealy et al., 1987; Ambrose, 1991; Kelly, 2000); however, more recent studies suggest these factors have little influence on the $\delta^{15}N$ values of animal tissues so they are not considered in this study (Murphy and Bowman, 2006; Hartman, 2011). An additional consideration is that the $\delta^{15}N$ values of some animals, such as rabbits, may be influenced by coprophagic activity. Irlbeck (2001) notes that coprophagy increases with decreasing food quality, i.e., lower protein content, which may be expected to occur with increasingly arid conditions. However, Ugan and Coltrain (2011) argue that this effect is counterbalanced by urea recycling, both of which are favored in more arid environments. While the effect is not resolved, we assume that if coprophagy influences $\delta^{15}N$ values it would vary with food quality resulting from vegetation/climate change. Therefore, $\delta^{15}N$ values might be expected to change in the same direction with climate whether or not coprophagy was being expressed.

Carbon

The majority of the world's vegetation (>90%) follows the C_3 photosynthetic pathway. The remainder is split between the C_4 and crassulacean acid metabolism (CAM) pathways, both adaptations to hot, arid environments, primarily through increased water use efficiency and reduced photorespiration. C_3 plants have a mean $\delta^{13}C$ value of −27‰ (range −22‰ to −35‰), and C_4 plants have a mean $\delta^{13}C$ value of −13‰ (range −9‰ to −19‰) (O'Leary, 1988; Kohn, 2010). CAM plants have variable signatures, but typically fall closer to the C_4 range. Studies have shown that the carbon isotope composition of C_3 plants exhibit natural variations in response to a number of variables, including irradiance, temperature, salinity, nutrient levels, and moisture stress (Farquhar et al., 1989; Tiezen, 1991; Heaton, 1999). These values are incorporated into the tissues of the herbivores that eat them, with adjustments for fractionation due to trophic level enrichment and tissue type (Ambrose and Norr, 1993). Thus, differences in $\delta^{13}C$ values in herbivore tissue, e.g., bone collagen, allows us to detect changing vegetation patterns, and by extension, changing environmental conditions (e.g., Van Klinken et al., 1994). Though C_4 and CAM plants are relatively scarce in this region of the Snake River Plain today, higher $\delta^{13}C$ values may also signify decreasing C_3/C_4-CAM vegetation ratios in the past (DeNiro and Epstein, 1978; Cerling and Harris, 1999; Passey and Cerling, 2006).

Factors controlling C4-CAM plant distributions

As changing C_3/C_4-CAM vegetation ratios are hypothesized with changing climate, we review the factors that influence the distribution of C_4-CAM plants, and their current prevalence on the Snake River Plain.

C_4 grasses comprise approximately half of the total number of known grass species, while C_4 dicots (shrubs and forbs) are much less common, making up less than 1% of total dicot species, and typically comprise less than 5% of flora within any ecosystem supporting them (Ehleringer et al., 1997). C_4 distribution is governed by multiple primary constraints, depending on the class of plant in question. The three climatic variables most correlated with C_4 distribution in time or space are concentration of atmospheric CO_2, temperature, and aridity. Studies have shown the following relationships:

1. C_4 plants increase with decreasing CO_2 due to more efficient CO_2 capture, which gives them a competitive advantage over C_3 plants (Ehleringer et al., 1997; Connin et al., 1998).
2. C_4 grass diversity has a strong positive relationship with growing season temperatures (highest correlation is with minimum July temperature). According to Teeri and Stowe (1976), in examining 27 regions of North America, temperature explained more than 90% of the total C_3/C_4 grass distribution across most geographic regions. Total precipitation was not as important in explaining this distribution, but summer precipitation would be required to initiate and, to some extent, sustain, plant growth.
3. In contrast, C_4 forb and shrub (dicot – e.g. *Atriplex* spp.) diversity and abundance increase with aridity. Temperature does not inform on C_4 dicot distribution as much as aridity measures such as summer pan evaporation rates and annual dryness ratios. According to Stowe and Teeri (1978), summer pan evaporation rates alone explained over 90% of C_4 dicot distribution in North America.

Based on stable carbon isotope data in Pleistocene fossil horse teeth recovered from various localities across the New World, MacFadden et al. (1999) found a latitudinal gradient in C_3/C_4 grass dominance, with the transition from C_4 to C_3 beginning around 45°N (data for the southern hemisphere is scant, but appear to follow the same trend). This is supported by data on modern (AD 1901–1971) C_4 grass distributions compiled by Teeri and Stowe (1976). Both studies indicate latitudinal changes in temperature are the driving cause of this gradient. The Snake River Plain falls between 42 and 44°N, suggesting C_3 dominance though with C_4 potential.

Little information is available regarding the specific distribution of C_4 plants on the eastern Snake River Plain. We used the list provided in Ehleringer et al. (1997:287) of genera known to undergo C_4 photosynthesis to compile an inventory of potential species. Supplementary Table 1 identifies plants from these genera with a recorded presence on at least some portion of the eastern Snake River Plain, compiled from the United States Department of Agriculture, Natural Resources Conservation Service's Online Plants Database. We noted 32 species from 18 genera: 8 forbs, 5 shrubs, and 19 grasses. Three of these are listed as introduced. Overall, there are currently relatively few C_4 species; those present have more restricted ranges than C_3 plants and reside within a few suitable microhabitats within the dominant sagebrush steppe plant community, primarily areas with high salt concentrations such as alkali flats or marshes.

For CAM plants there are 8 species from 4 genera currently found on the eastern Snake River Plain (Supplementary Table 1); 2 are listed as introduced. As with the C_4 species, most CAM plants are restricted in their distribution, being either confined to open, rocky habitats or near water sources. Plain's Prickly pear (*O. polyacantha*) is currently the most common CAM plant on the Snake River Plain. Isotopic studies of this species and others within the genera provide an average $\delta^{13}C$ range of −12.7 to −14.3‰ (Eickmeier and Bender, 1976; Orr et al., 2015), placing it within the isotopic range of C_4 plants. The distribution of this plant is governed by water availability, with the greatest occurrences noted in arid to semi-arid areas with low but frequent precipitation events (Eickmeier and Bender, 1976; Dougherty et al., 1996; Lauenroth et al., 2009). Due to its shallow root system, this plant has the advantage of being able to utilize low levels of rainfall, i.e., 2.5–5 mm or rainfall capable of permeating only the upper 10 cm of soil. This advantage is enhanced by its ability to store this water for longer terms than other plants in the same environment. Likely due to its higher level of water use efficiency, the plains prickly pear is currently more widespread across the Snake River Plain than C_4 plants.

Feeding ecology of pygmy rabbits, pocket gophers and ground squirrels

Pygmy rabbits, pocket gophers and ground squirrels were chosen for this initial study as they contained the largest sample size throughout the stratigraphic sequence, and were the primary indicators of environmental change in previous studies (Butler, 1969; Guilday, 1969). While one species may have imparted enough information to test our hypothesis, multiple taxa were utilized to assess the response of animals of different feeding ecology to the proposed changing climatic conditions.

Pygmy rabbits

Pygmy rabbits are considered sagebrush-obligates, but as with all species in cold desert habitats feeding patterns are variable throughout the year depending on available food sources. Based on studies of pygmy rabbits in southeastern Idaho, Green and Flinders (1980) observed dietary proportions of 51% shrubs, 39% grasses, and 10% forbs between late spring and fall (May through October), though in winter (November through February) and early spring (March through April) diet consisted almost entirely of sagebrush (99% and 80%, respectively). Antelope bitterbrush (*Purshia tridentata*) and gray rabbitbrush (*E. nauseosa*) were recorded at very low frequencies annually (~1 and <1%, respectively), indicating that sagebrush was nearly exclusively the shrub of choice. Annually, these authors estimate a diet of 67% shrubs, 26% grasses, and 6% forbs. While pygmy rabbits construct or utilize burrows these typically extend only 1 m in depth (Green and Flinders, 1980); the relatively short length of these tunnels suggests below ground plant parts are of lower significance in diet.

Pocket gophers

In contrast to pygmy rabbits, pocket gophers and to an extent, ground squirrels are identified as true generalist herbivores. Verts and Carraway (1999) summarize studies of feeding habits for pocket gophers in surrounding states, and indicate they consume most any above and below ground vegetal material. Dietary proportions ranged between 40 and 90% for forbs, 1 and 50% for grasses, and 1 and 8% for shrubs, depending on season and local availability. Forbs are the most important source, but grasses, succulents, shrubs and trees are utilized when present or as needed. Roots and tubers of some plants are commonly foraged, usually obtained via 45–60 m tunnel systems characteristic of this species (Verts and Carraway, 1999). Succulents, especially prickly-pear cactus, a plant utilizing CAM photosynthesis, are highly utilized when available. In general, diet typically consists of above ground parts during the spring and summer and below ground parts during the fall and winter.

Ground squirrels

Townsend's ground squirrels undergo estivation, typically entering dormancy in late spring/early summer until late winter (7.5–9 months) (Rickart, 1987). For the few months they are active, they consume primarily green vegetation and seeds. In their study of a population of Townsend's ground squirrels in southwestern Idaho, Smith and Johnson (1985) note that diet consisted primarily of grasses (60%: 51% leaves, 9% seeds), with the remainder made up of forbs (21%: 16% leaves, 5% seeds), shrub leaves (16%), and unlike pygmy rabbits and pocket gophers, insects (2%). While their burrows extend an average of 17 m, below ground plant parts do not appear to contribute significantly to diet.

As the sample includes a dietary specialist, a generalist, and a generalist that undergoes estivation, we expect isotopic differences between these species as a whole, and potential differences in responses to climate perturbations during the Holocene.

Materials and methods

A total of 182 mandibles or tibia from separate individuals (78 pocket gophers, 81 pygmy rabbits, 23 ground squirrels) from nine arbitrarily defined 10 cm excavation levels were examined. The majority of the material was chosen from Block E2B, from which they were identified to species previously (Guilday, 1969). However, sample sizes for the upper layers in this block were small, and all mandibles had been soaked in a varnish. To avoid potential contamination by the varnish and to get a larger sample we selected material from several nearby blocks for the upper layers of the site. In addition, Block E2B terminated at a depth of 400 cm. To include the basal layers of the site in our analyses we selected samples from Block E3D, within which the lowest levels of excavation were reached. The stratigraphy of the site and locations of these blocks are discussed in Butler (1968) and Burnett (1976). Stratigraphic integrity was evaluated by examining the stratigraphic profile maps for each unit, and through radiocarbon dates of bone samples throughout the stratigraphic sequence.

Due to their small size, mandibles and tibia were processed whole using methods outlined in Misarti et al. (2009) and Matheus (1997). Samples were sonicated in ultrapure water to remove any soil or debris and air dried. Lipids were removed by soaking the bone in a 2:1 chloroform-methanol solution (after Bligh and Dyer, 1959) for 8 h. Samples were then demineralized in a 6 N HCl and $18.2\Omega H_2O$ solution (~1 N HCl) over the course of 1–6 days at 4 °C. After rinsing to neutral pH in $18.2\Omega H_2O$, samples were placed in a 5% KOH: $18.2\Omega H_2O$ solution for ~8 h at room temperature to remove potential humic contamination from the surrounding soils. Samples were again rinsed to neutral pH, and the remaining material was gelatinized on a vortexer at approximately 65–70 °C in a weak HCl solution (~0.01–0.02 N HCl) blown with N_2 gas. Samples were then filtered using Millex-HV 0.45 μm filters and freeze dried for 48 h. Between 0.4 and 0.5 mg of collagen was weighed for analysis. The $\delta^{13}C$ and $\delta^{15}N$ compositions were obtained using a Thermo Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS), with a ConFlo IV interface and Costech Elemental Analyzer (EA) at the Interdisciplinary Laboratory for Elemental and Isotopic Analysis (ILEIA) located at the Center for Archaeology, Materials and Applied Spectroscopy (CAMAS) on the campus of Idaho State University. Precision of these measurements is ±0.2‰ for $\delta^{13}C$ and ±0.2‰ for $\delta^{15}N$. All $\delta^{13}C$ and $\delta^{15}N$ values are reported conventionally versus the Vienna Pee Dee Belemnite (VPDB) (carbon) and air (atmospheric nitrogen) standards as:

$$\delta(‰) = 10^3 \cdot \left[R_{\text{sample}} \middle/ R_{\text{standard}} - 1 \right]$$

Samples with values outside of the accepted ranges of C/N (atomic %) and C and N % were excluded from this study (DeNiro, 1985; Ambrose, 1990). This includes those above or below the C/N range of 2.9–3.6, the carbon concentration of 15.3–47% and the nitrogen concentration of 5.5–17.3%.

Nine collagen samples extracted following the protocols described above were submitted for AMS ^{14}C dating at the Lawrence Livermore National Labortaory in addition to the isotope analyses. Radiocarbon age calibrations were conducted in Clam v2.2 (Blaauw, 2010) using the Intcal13.14c calibration curve (Reimer et al., 2013), with ranges reported at the 95% confidence interval. An age-depth model was also created in Clam v.2.2 using linear interpolation and the Intcal13.14c calibration curve (Reimer et al., 2013).

Data analysis

Differences between species and with depth were analyzed using one-way analysis of variance (ANOVA) with Tukey's HSD post hoc tests when variances were equal. When variances were unequal, Welch's ANOVA with Steel-Dwass nonparametric comparisons for all pairs was employed. As the carbon isotope compositions for the gophers were not normally distributed, all carbon data were normalized using the Box Cox Y Transformation (using the best transformation). All analyses were performed in JMP 12.0 (SAS Institute, Cary, NC, USA) with significance set at $p < 0.05$.

Results

Of the 182 samples analyzed, 169 yielded data within acceptable C/N, and C and N % (Supplementary Table 2) indicating the well preserved nature of the deposit. Thirteen samples were discarded from analysis due to C/N above 3.6 ($n = 4$), and C or N % below normal ranges ($n = 9$).

Dating

The radiocarbon results are provided in Table 1 and Figure 3. These include radiocarbon ages previously obtained through funding for the excavations in the 1960s along with dates obtained under the present project. Based on analyses of its physical properties Layer 15 is defined as a deposit of Mazama Ash (Ore, 1968), a discrete event found in numerous deposits in the Pacific Northwest, currently dated to 7550 cal yr BP (Hallett et al., 1997; Zdanowicz et al., 1999). The distributions of dates generally suggest a dramatic decline in sedimentation rate above the Mazama tephra, as previously reported (Butler, 1972).

There are some age reversals downsection in the upper layers (Layers 11 through 13). A review of the stratigraphy of specific block profiles in the original field notes indicates significant human disturbance in the upper levels in Blocks E3C and E1B which likely resulted in mixing of faunal material; this is reflected in the anomalously old dates for faunal material from the upper layers of these units. After evaluating the sediment profiles for the various blocks in light of disturbance and mixing, we rejected the radiocarbon ages and removed all the stable isotope data from Blocks E1B, E2A, E4A, and E4C, and material from Layer 13 from Block E3C from further analyses to reduce the potential incorporation of disturbed materials. This adjustment results in a total of 142 samples from eight levels (see Table 2 for a breakdown of species by level). An age-depth model was created by first rejecting the anomalously old radiocarbon ages from the reworked blocks described above. We also rejected two previously reported ages. One represents an anomalously young age below the Mazama tephra (M-1853); this sample has large error and was obtained from a bone without appropriate pre-treatment. The second sample (WSU-561, sample 67-1) has a very large error associated with it (±575 yrs) so a new age was obtained for that level to refine the chronology. Age ranges for each depth interval were then obtained using linear interpolation in Clam 2.2 (Blaauw, 2010) (Fig. 3). Age ranges represent the 95% confidence intervals for the upper and lower boundary of each level.

Stable isotope data

The overall range of $\delta^{13}C$ values (Figs. 4 and 5) for pocket gophers is −23.0 to −13.1, with an average of −20.1; for pygmy rabbits −22.4 to −19.7 with an average of −21.1; and for the ground squirrels −21.6 to −16.7 with an average of −19.4. The $\delta^{15}N$ range for pocket gophers is 3.6–11.0, with an average of 7.5; for pygmy rabbits 4.4 to 9.9 with an average of 7.3; and for the ground squirrels 3.9 to 10.4 with an average of 6.3.

A one-way ANOVA of $\delta^{13}C$ and $\delta^{15}N$ values by species reveals significant differences in both $\delta^{13}C$ [Welch's $F(2,58.80) = 24.45$, $p < 0.001$] and $\delta^{15}N$ [Welch's $F(2,57.58) = 5.70$, $p = 0.006$]. For nitrogen, a Steel-Dwass multiple comparisons test reveals the significant differences lie between ground squirrels and pygmy rabbits ($p = 0.001$) and ground squirrels and pocket gophers ($p = 0.008$), with the squirrels having consistently lower $\delta^{15}N$ values than the other two species. For carbon, a Steel-Dwass multiple comparisons test reveals the significant differences lie again between ground squirrels and pygmy rabbits ($p < 0.001$) and ground squirrels and pocket gophers ($p = 0.009$), with ground squirrels having consistently higher $\delta^{13}C$ values than the other two species.

ANOVAs with post hoc tests were run to identify significant differences in $\delta^{13}C$ and $\delta^{15}N$ values between layers for each species (Table 3). For gophers, significant differences were observed with depth for both nitrogen ($F(6,48) = 6.009$, $p < 0.001$) and carbon (Welch's $F(6,18.33) = 2.67$, $p = 0.049$). The squirrels show significant differences with depth for nitrogen ($F(2,20) = 5.91$, $p = 0.010$), but not for carbon ($F(2,20) = 1.65$, $p = 0.218$). For rabbits, significant differences were observed with depth for both carbon ($F(7,56) = 2.49$, $p = 0.027$) and nitrogen ($F(7,56) = 2.45$, $p = 0.029$).

For both rabbits ($p = 0.037$) and gophers ($p = 0.038$), the only significant differences in $\delta^{13}C$ values lie between Layer 16:140-150 and the Base layer. Significant differences in $\delta^{15}N$ values were observed between some layers for all species. Gophers show differences in Layer 14 with those below (16, 18, and Base), and Layer 16 with those below (18 and Base). Rabbits showed differences between each layer and the Base layer, though only Layers 40–50 and 14:90-100 versus the Base layer provided a p-value below 0.05. Squirrels showed significant differences between the youngest and oldest layer.

Discussion

Stable isotope signatures, feeding ecology and diet

The isotopic results reveal differences related to feeding ecology among the three species examined, and changes in diet composition over time. In the discussion below, we assume a trophic level fractionation factor of 3‰ for nitrogen (Schoeninger and DeNiro, 1984; Ambrose, 1991; Vanderklift and Posnard, 2003) and negligible diet-tissue fractionation. We use −29‰ for C_3 and −14.5‰ for C_4-CAM for the carbon endmembers. The C_3 endmember is based on $\delta^{13}C$ values for sagebrush collected around the cave site in 2011 (−29.0‰ ± 0.8), while the C_4-CAM endmember is based on values for plains prickly pear collected around the site in 2011, and four-wing saltbush (*Atriplex canascens*) collected near Pocatello, Idaho that same year (−14.5‰ ± 0.8) (Supplementary Table 3). We

Table 1
Radiocarbon dates for layers spanning the interval of samples analyzed for stable isotopes at the Wasden Site, including those from bone collagen samples obtained during the current project[c].

Lab#	Sample ID	Layer	Block	^{14}C age yr BP	δ^{13}C (‰)	Cal age ranges (2 sigma)[a]	Material dated	Reference
CAMS-157224	SI13.6	Layer 13 (30–39 cm depth)	E2B	1935 ± 25	−21.9	cal BP 1823–1931	Rabbit bone collagen	Current study
CAMS-154786	3868.PR.6	Layer 14 (40–50 cm depth)	E3C	3075 ± 30	−21.5	cal BP 3211-3364	Rabbit bone collagen	Current study
CAMS-159529	3401.PR.5	Layer 14 (75 cm depth)	E3B	5890 ± 35	−20.5	cal BP 6645-6787	Rabbit bone collagen	Current study
CAMS-154788	TT14.5	Layer 14 (90–100 cm depth)	E2B	6050 ± 25	−14.7	cal BP 6799-6976	Gopher bone collagen	Current study
	Mazama Ash	Layer 15 (~100–110 cm depth)	Not Provided	6730 ± 40	Not reported	cal BP 7514-7665	See references	Hallett et al., 1997; Zdanowicz et al., 1999
WSU-641	67–4	Layer 16 (200–210 cm depth)	E2Z, E1B, E1A, E1C	7750 ± 210	Not reported	cal BP 8167-9130	Charcoal	Butler 1968
CAMS-159487	TT16.5	Layer 16 (200–210 cm depth)	E2B	8000 ± 25	−20.9	cal BP 8774-8998	Gopher bone collagen	Current study
WSU-560	67–2	Layer 18 (253 cm depth, Feature 89)	Not Provided	8160 ± 260	Not reported	cal BP 8429-9596	Charcoal/burned microfauna	Butler 1968
CAMS-157225	SI18.9	Layer 18 (340–350 cm depth)	E2B	8675 ± 25	−20.4	cal BP 9549-9680	Rabbit bone collagen	Current study
CAMS-154789	SISM.10	Base (424–435 cm depth)	E3D	8910 ± 25	−21.3	cal BP 9917-10177	Rabbit bone collagen	Current study
Rejected Dates[b]								
CAMS-154785	3359.PR.2	Layer 11 (<30 cm depth)	E1B	5695 ± 25[1]	−19.4	cal BP 6409-6538	Rabbit bone collagen	Current study
CAMS-154787	L13.5	Layer 13 (35–39 cm depth)	E3C	5990 ± 25[1]	−14.1	cal BP 6749-6892	Gopher bone collagen	Current study
WSU-561	67–1	Layer 13 (39–43 cm depth; Feature 64)	Not Provided	3340 ± 575[2]	Not reported	cal BP 2348-5271	Charcoal	Butler 1968
M-1853		Layer 16	Not Provided	7180 ± 350[1,3]	Not reported	cal BP 7422-8773	Bison bone collagen	Butler 1968

[a] Calibrations conducted in Clam v2.2 (Blaauw, 2010) using the Intcal13.14c calibration curve (Reimer et al., 2013).
[b] Rejected dates include those that fall off the trend defined by other nearby dates[1] (see Fig. 3 and discussion in text), dates with large uncertainty[2], and dates obtained on bone samples prior to the development of appropriate pre-treatment methods for collagen extraction and purification[3]. All samples from Layer 11, Block E1B and Layer 13, Block E3C were removed from analysis due to age reversals likely due to reworking as discussed in the text.
[c] Age-depth model using these dates is provided in Figure 3.

assume a diet-tissue fractionation of ~5.0‰ (Ambrose and Norr, 1993; Ambrose et al., 1997) and a +1.9‰ correction for the Suess effect (Long et al., 2005; Verburg, 2007) for carbon. With this model, a δ^{13}C value of ~ −22‰ for bone collagen is consistent with an animal subsisting solely on C_3 plants, while significantly higher values are likely indicative of the dietary incorporation of C_4 and/or CAM plants.

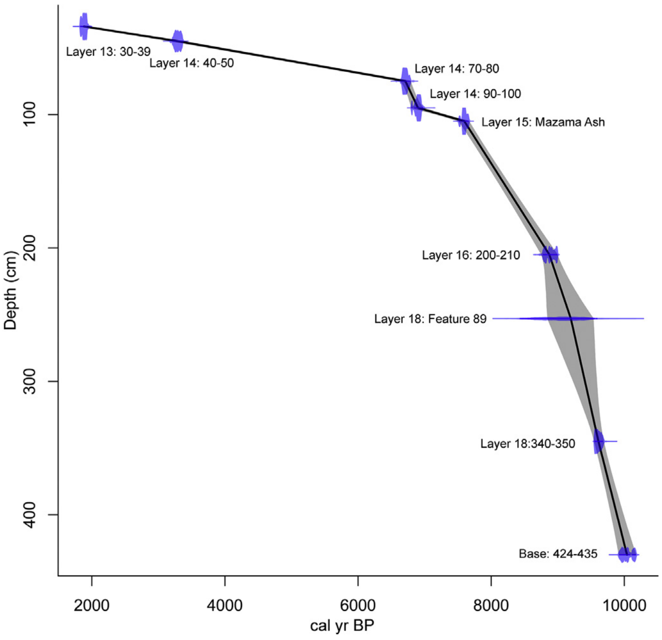

Figure 3. Age-depth model for the Wasden Site. Rejected ages identified in Table 1 were excluded from the model. The age-depth model was created in Clam 2.2 (Blaauw, 2010) using linear interpolation and the Intcal13.14c calibration curve (Reimer et al., 2013). The model was created with 10,000 iterations and used calendar age point estimates for depths based on a weighted average of all age-depth curves. The gray-shaded area represents the 95% CI. Calibrated age distributions (95%) for the individual dates included in the model are shown at their corresponding depths.

Pygmy rabbits

The δ^{13}C and δ^{15}N data for pygmy rabbits clearly show a tighter clustering than the gophers or ground squirrels (Fig. 4), in line with expectations for a dietary specialist. As sagebrush is the dominant food source for this species, we tentatively conclude from the mean value and restricted range of collagen δ^{13}C values that the stable isotope values of the pygmy rabbits largely reflect those of sagebrush.

The pygmy rabbit δ^{15}N data is relatively high, indicating a high plant-soil nitrogen isotope baseline in this region. In general, this is consistent with broad-scale relationships between climate and soil/plant δ^{15}N ratios (Amundson et al., 2003; Craine et al., 2009), given the climate conditions in this arid region (precipitation is currently ~250 mm a^{-1}). The mean δ^{15}N values of pygmy rabbits, pocket gophers and ground squirrels are generally similar during each time interval, though the gophers tend to have higher variance (Fig. 4). Of note is that while rabbits are known to perform coprophagy, which theoretically should increase δ^{15}N values due to increased digestive efficiency, the δ^{15}N values of the pygmy rabbits fall between those of the gophers and squirrels. This suggests that either: 1) coprophagy has little influence on δ^{15}N values in bone collagen or is counterbalanced by urea recycling, as proposed by Ugan and Coltrain (2011); 2) coprophagy is being expressed but gophers are consistently consuming plants with higher δ^{15}N values, masking its effect; or 3) differences in dietary protein quality and quantity are resulting in different nitrogen discrimination factors between species (Sponheimer et al., 2003; Robbins et al., 2005; Poupin et al., 2014), again masking effects of coprophagy.

Pocket gophers and ground squirrels

As these generalist herbivores consume a wide range of available plants, their stable isotope values have the ability to better track plant diversity compared to pygmy rabbits, including CAM and C_4

Table 2
Number of faunal samples selected for temporal analysis following analytical and stratigraphic screening.

Layer	Depth (cmbs)	*Calculated age range for depth interval*[a]	*Thomomys cf. talpoides*	*Brachylagus idahoensis*	*Spermophilus townsendii*	Total/Layer
13	30–39	1286-2570 BP	0	10	10	20
14	40–50	2594-3920 BP	5	5	0	10
14	70–80	6085-6818 BP	5	5	0	10
14	90–100	6779-7298 BP	9	10	4	23
16	140–150	7974-8241 BP	8	10	0	18
16	200–210	8695-9029 BP	9	8	0	17
18	340–350	9527-9709 BP	10	7	0	17
Base	424–435	9901-10205 BP	9	9	9	27
			55	64	23	142

[a] Age range based on interpolated dates obtained from the Clam age-depth model for the 95% CI of the upper and lower boundary of the levels.

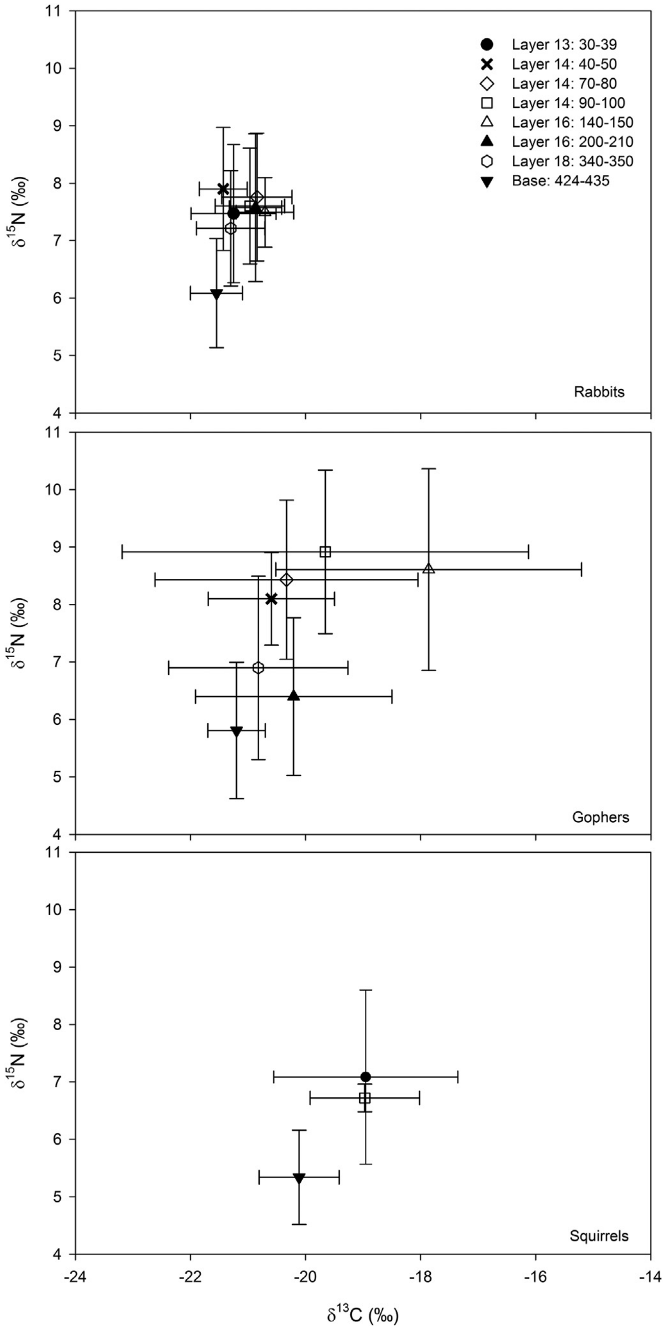

Figure 4. Bi-plots of mean bone collagen δ^{13}C and δ^{15}N values by species and layer. 1σ error bars shown.

plants (Fig. 4). Thus, the observed broad and varying δ^{13}C ranges in these animals is best explained by C_4-CAM diet contributions, which change over time. In general, the δ^{13}C data suggests higher values and greater variance during a period centered around 8000 cal yr BP (Fig. 5), with lowest values and variance prior, and moderate values and variance afterward. Based on a simple, 2-carbon endmember, linear mixing model with endmembers of −22.1‰ (C_3) and −7.6‰ (C_4-CAM), the periods of relatively high δ^{13}C ratios at ~8000 cal yr BP would predict an average C_4-CAM diet of 25% with some individuals having C_4-CAM contributions of more than 50%. These data suggest different plant communities in the past relative to modern undisturbed areas of the eastern Snake River Plain.

Interestingly, the ground squirrels had consistently lower δ^{15}N values than the other two species. Previous research found heavier δ^{15}N values in metabolically active tissues of nutritionally stressed or fasting animals, hypothesized as the result of incorporation of enriched nitrogen during protein synthesis due to lack of exogenous input and necessary catabolic breakdown and recycling of existing body proteins (Hobson et al., 1993). With this model we would expect the squirrels to have higher δ^{15}N values as they undergo estivation for long periods of time, reducing the input of dietary nitrogen and increasing internal cycling of existing compounds. However, as Lee et al. (2012) observed, only tissues actively synthesizing proteins during estivation would exhibit higher δ^{15}N values. In their study of hibernating arctic ground squirrels, Lee et al. (2012) found increases in δ^{15}N values in organ tissues (liver, heart, brown adipose tissue and small intestine), but not in the different skeletal muscles, presumably due to little or no protein synthesis in those tissues during hibernation. The relatively low δ^{15}N values in our ground squirrels may be the result of reduced collagen synthesis during torpor. The δ^{15}N values in squirrel bone collagen would therefore primarily represent the period when they are active and feeding, which is the spring and early summer, when precipitation is higher and δ^{15}N values of the available plants might be lower.

Trends in stable isotope signatures and paleoclimate inferences

Overall, the δ^{13}C and δ^{15}N values for the Base Layer (424–435 cm depth; 9901–10,205 cal yr BP) are more distinct from all other layers, containing the lowest average values (Figs. 4 and 5). Pollen records from southern and central Idaho (and Northern Utah) generally show that the vegetation change near the beginning of the Holocene was larger than subsequent changes, and infer a transition to warmer and drier conditions from the preceding deglaciation (e.g., Bright, 1966; Beiswenger, 1991). The isotopic shift is consistent with this inference as current global patterns show a positive relationship between δ^{15}N value (of soils and plants) and mean annual temperature, and a negative relationship with mean annual precipitation (Amundson et al., 2003; Craine et al., 2009).

Values for δ^{15}N continue to increase until ~7000 cal yr BP, after which time there is no clear trend. As mentioned above, this

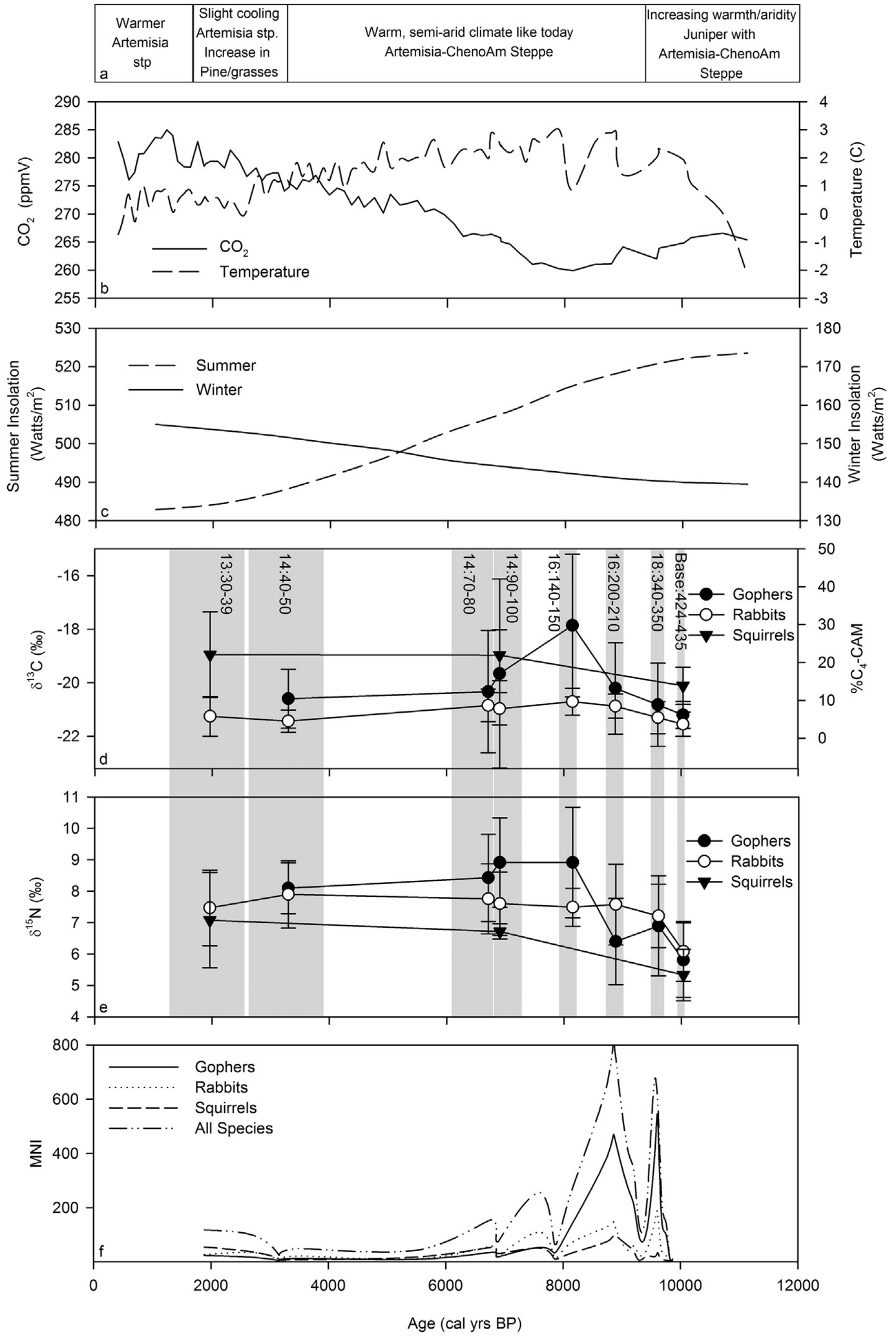

Figure 5. a) General climate/vegetation regime based on Swan Lake pollen core (Bright, 1966); b) Holocene average atmospheric CO_2 reconstructed from the Taylor Dome ice core in Antarctica (Indermühle et al., 1999) and temperature (given as deviations from present values) derived from $\delta^{18}O$ from the Agassiz and Renland core sites in Greenland (Vinther et al., 2009); c) summer and winter insolation (Berger and Loutre, 1991); d) mean $\delta^{13}C$ and $\%C_4$ by species(1σ error bars shown); e) mean $\delta^{15}N$ by species(1σ error bars shown); and f) MNI for each species and total MNI (all species) for each layer in Block E2B, as recorded by Guilday (1969). Shaded areas represent the calibrated age ranges for each level analyzed.

increasing trend may suggest increasing warmth and/or aridity through the mid-Holocene. While not well-defined, the data for rabbits seem to show a decline in $\delta^{15}N$ values upwards to Layer 13, dated to ~1900 cal yr BP. Although the differences between Layer 13 and the preceding layers (aside from the Base layer; Table 3) are not significant, this apparent trend would fall in line with decreasing temperatures and/or increasing precipitation during the Neoglacial. While suggestive, more samples are needed to better define any trends.

As mentioned above, unequal variances in carbon isotope compositions between the various layers were observed for gophers, with the trend towards increasing variance until 7000 cal yr BP, followed by a decrease (Figs. 4 and 5). This change in variance provides an effective measure for the incorporation of a broader range of $\delta^{13}C$ values, thus reflecting changing ratios of C_3/C_4-CAM vegetation on the landscape. Specifically, we see a stronger presence of C_4-CAM vegetation in Layer 16 and the lower levels in Layer 14. Ground squirrels appear to have consistently higher $\delta^{13}C$ values

Table 3
Significant differences in δ^{13}C and δ^{15}N values between levels by species (in bold). All p-values < 0.10 shown, - indicates p-value is greater than 0.10.

	Level	13:30-39	14:40-50	14:70-80	14:90-100	16:140-150	16:200-210	18:340-350	Base:424-435
Gophers	14:40-50	N/A							
	14:70-80	N/A	–						
	14:90-100	N/A	–	–					
	16:140-150	N/A	–	–	–				
	16:200-210	N/A	–	–	δ^{15}N (**0.008**)	δ^{15}N (**0.039**)			
	18:340-350	N/A	–	–	δ^{15}N (0.055)	δ^{13}C (0.095)	–		
	Base:424-435	N/A	δ^{15}N (0.084)	δ^{15}N (**0.029**)	δ^{15}N (**0.001**)	δ^{15}N (**0.004**) δ^{13}C (**0.038**)	–	–	
Rabbits	13:30-39								
	14:40-50	–	–						
	14:70-80	–	–						
	14:90-100	–	–	–					
	16:140-150	–	–	–	–				
	16:200-210	–	–	–	–	–			
	18:340-350	–	–	–	–	–	–		
	Base:424-435	δ^{15}N (0.085)	δ^{15}N (**0.049**)	δ^{15}N (0.096)	δ^{15}N (**0.043**)	δ^{15}N (0.069) δ^{13}C (**0.037**)	δ^{15}N (0.085)	–	
Squirrels	13:30-39								
	14:90-100	–	N/A	N/A		N/A	N/A	N/A	
	Base:424-435	δ^{15}N (**0.008**)	–	–	–	–	–	–	

than the gophers and rabbits, suggesting greater C4-CAM input, but more samples and levels are needed to evaluate this pattern. In contrast, pygmy rabbits overall cluster tightly in the C_3 range with little variance through time.

In the case of the pygmy rabbits, we interpret their δ^{13}C values to reflect primarily sagebrush, and not variable contributions of plants with different photosynthetic pathways as the δ^{13}C values overall tend to cluster tightly within a relatively narrow range. If this is true, then the relatively higher δ^{13}C values may correspond to periods of greater water stress, when leaf stomata tend to be more closed, reducing the amount of CO_2 available for photosynthesis leading to less discrimination and enrichment in the heavy isotope (Farquhar et al., 1989; Evans and Black, 1993). In other words, the significant increase observed between the Base layer and Layer 16 may be indicative of increasing aridity, consistent with the inference from the increase in ^{15}N. For the pocket gophers, the lack of any clear C_4-CAM signal in the Base layer, the appearance of a signal indicative of mixed vegetation types in Layer 16, and of high C_4-CAM signals in the lower levels of Layer 14 suggest that C_4-CAM vegetation increased in relative abundance, and as such there was likely an increase in encounter rates while feeding.

While tentative, we can make some further paleoclimatic inferences from the isotopic dataset based on known relationships between C_4-CAM distributions and environmental conditions. According to a model provided by Ehleringer et al. (1997), there is a crossover temperature at which photosynthetic efficiency (in terms of quantum yield) is greater in C_3 versus C_4 plants for a given atmospheric CO_2 concentration. At ~20 °C the average crossover (between C_4 monocots and dicots) occurs at ~300 ppmv; atmospheric CO_2 concentrations greater than this generally favor C_3 and concentrations lower favor C_4. While the CO_2 concentrations throughout the Holocene shift by only ~25 ppmv, the observed concentration range (~260–285 ppmv) is below the ~300 ppmv threshhold, and relatively low values occur during the time of maximum δ^{13}C. Further, regional and Northern Hemisphere paleoclimate data suggest relatively warm summer temperatures during the time of high δ^{13}C signatures (Teeri and Stowe, 1976). Either warmer summers or lower CO_2, or both, may have been sufficient to promote the expansion of C_4 plants (Fig. 5). Lastly, Stowe and Teeri (1978) observed summer pan evaporation rates and annual dryness ratios as the dominant influence on C_4 forb/shrub distributions. Their requirement for summer precipitation, combined with evidence for increased aridity, could be explained by increased summer and decreased winter precipitation. The implication of changes in the seasonality of precipitation is consistent with known changes in summer and winter insolation (Fig. 5; Anderson, 2012).

Based on this information, the changing δ^{13}C signatures from ca. 10,000 to 7000 cal yr BP in the gophers and squirrels suggests increasing abundance of either C_4 or CAM (most likely the plain's prickly pear) plants, or both, during this time period. Ecological considerations for both plant types suggest the higher δ^{13}C values, i.e., stronger C_4-CAM signals, in Layers 14 and 16 are the result of a change towards more arid and potentially warmer climates during the mid-Holocene. The trend towards aridity, and perhaps changing seasonal distribution of precipitation (greater in summer), is supported by the overall trend in δ^{15}N values and the trend of increasing δ^{13}C ratios in the rabbits (and by extension, sagebrush) discussed above, likely reflecting moisture stress. A significant change in climate or environment around the site during the mid-Holocene is also supported by the small mammal abundance data tabulated by Guilday (1969) for Owl Cave. We see a decline in total abundance as well as gopher abundance specifically after ~8000 cal yr BP (Fig. 5), indicating conditions were not as suitable to support large populations as they were in the preceding years. The change in sedimentation rate pre- and post- Mazama, as inferred from the age-depth relation (Fig. 3), also indicates substantial mid-Holocene climate and/or environmental change. Additional lines of evidence for this trend can be found in other climatic records for the Snake River Plain and surrounding region as discussed below.

Comparison to other records of paleoenvironmental change on the Snake River Plain

There have been several significant studies focused on environmental change through the Holocene period in southeastern Idaho. Through analysis of changing proportions of plants such as *Artemisia*, *Pinus*, *Juniperus*, Chenopodiaceae/Amaranthaceae, and Poaceae [Gramineae], in pollen from cores from Swan Lake, located at the northern point of ancient Lake Bonneville, Bright (1966) noted increasing warmth and aridity beginning around 13,200 cal yr BP, and climaxing at ~ 9400 cal yr BP. This was followed by a lengthy, warm, somewhat arid period until 3300 cal yr BP, during which vegetation was similar to present. A return to slightly cooler conditions was then observed until 1600 cal yr BP, after which temperature increased and settled on conditions similar to today (Fig. 5).

A similar trend was observed by Beiswenger (1991) at Gray's Lake on the eastern border of the Snake River Plain. Using the same plant types as indicators, Beiswenger (1991) observed increasing warmth and aridity after the Pleistocene/Holocene transition, climaxing ~9100 cal yr BP. Slight cooling and/or increased precipitation is suggested between 7900 and 2000 cal yr BP.

Additional lines of evidence have been obtained from lava tube sediments (Bright and Davis, 1982; Davis et al., 1986) and woodrat middens (Bright and Davis, 1982) near the Wasden Site. Both studies note a predominance of plants more adapted to warmer, arid habitats (Chenopodiaceae/*Amaranthus*) just below a deposit of Mazama Ash above which plants more adapted to cooler and/or moister conditions predominate (*Pinus*, Poaceae [Gramineae]). They interpret this as an incursion of shadscale steppe into sagebrush steppe ecotones between the Pleistocene/Holocene transition, climaxing around 7500 cal yr BP.

These data taken together are generally consistent with the isotope compositions of the rabbits, gophers and squirrels, along with physiological parameters of C_4 and CAM plants, which suggest increasing aridity and possibly temperature from the beginning of the record ~ 10,000 until ~7000 cal yr BP. The presence throughout the record of pygmy rabbits, which are sagebrush obligates, indicates continual sagebrush habitat. Though C_4-CAM plants likely increased, they were probably not dominant. Such a mixed habitat requires climatic conditions within the tolerance levels of both C_3 and C_4-CAM plants. One possible explanation is an increase in prickly-pear cacti, as they can thrive in more arid precipitation regimes than C_3 plants. Either alternatively or in conjunction with increases in prickly pear, we may be seeing an incursion of C_4 dicots (shrubs/forbs) as opposed to grasses. C_4 dicots can handle more variation in temperature than C_4 grasses, and more variation in precipitation than many C_3 plants. C_4 dicots such as *Atriplex* species shadscale or saltbush have been observed in midden from cave sites near the Wasden Site dating to the early and mid-Holocene, suggesting they could contribute to the C_4 content in our sample.

Considerations for future research

Greater sample resolution is needed to better define the $\delta^{13}C$ and $\delta^{15}N$ distributions, especially from the mid-Holocene to present. The site was excavated in discrete 10 cm levels, however, based on differences in depositional rates each level represents greatly varying time periods. While some ‘time-averaging’ is desired for interpretations made from conventional analyses of faunal distributions, i.e., using species minimum number of individuals [MNI] and number of identifiable specimens [NISP], as it reduces the effect of short-term, natural fluctuations in abundances of small mammal populations (Terry, 2008a, 2010b), it introduces greater variability in the results for chemical analyses. Dating of multiple samples per layer would also help refine age ranges and identify potential disturbance. As the data suggest significant ecological changes occurred during the early Holocene, better chronological control and increased sample resolution would enhance paleoclimatic interpretations. Lastly, isotopic values for modern analogs of the species in this study would enable the evaluation of changes in the paleoenivronmental data relative to modern climate. Extending this paleoclimate record up to the present would allow for a better assessment of our inferred Holocene climatic conditions relative to the instrumental period. However, the Wasden site is challenged in this regard as owl pellet deposition rates have slowed, and the vegetation at the site now is altered by invasive species and agriculture.

Conclusions

The isotopic analysis of a sample of the small mammal remains from the Wasden Site in SE Idaho reveals the fidelity of bone collagen isotopic signatures regarding feeding ecology characteristics that can be exploited to learn about past environmental change. Significant temporal variability in isotopic composition are best explained by paleoenvironments different than today. The data are consistent with a trend towards increasing temperature and/or aridity between 10,000 and 7000 cal yr BP, and perhaps increased seasonality with relatively higher summer moisture. More data is required to assess the trajectory from the middle Holocene to present, as climate trended towards modern conditions. The increase in $\delta^{13}C$ and $\delta^{15}N$ values in the pygmy rabbits and pocket gophers and the presence of a strong C_4-CAM signal in the pocket gophers may all be indicative of less total precipitation and/or increased temperature, resulting in vegetation changes around the site, though the general similar trends in $\delta^{13}C$ and $\delta^{15}N$ values are consistent with aridity as a primary control.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.yqres.2016.03.008.

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